

Modeling Food Web Interactions: A Conceptual Framework and Applications for Managing Native-Nonnative Assemblages

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Introduction

Introductions or changes in abundance of nonnative species can threaten the ecological integrity of aquatic communities. Nonnatives frequently affect other species directly through predation or competition, or indirectly via alternative pathways through the food web. Even without direct trophic interaction, the distribution or behavior of species can be altered in response to predation risk (Eggers 1978; Clark and Levy 1988; Walters and Juanes 1993) or the presence of a superior competitor, consequently diminishing growth, survival, or reproduction of native species. Given the complex array of potential processes and interactions that can affect aquatic communities, a food web perspective is required for understanding how proposed or existing nonnative species introductions affect the structure and function of aquatic communities.

Bioenergetically-based food web models, when coupled with directed sampling for diet, growth, size structure, thermal experience, and estimates of relative or absolute abundance, provide an effective method for quantifying trophic interactions in a temporal, spatial, and ontogenetic framework (Ney 1990). By quantifying linkages in a food web, we can identify strong interactions that potentially regulate populations in aquatic communities (Brandt and Hartman 1993). For instance, by using this approach, we can evaluate the carrying capacity of a system and identify potential seasonal bottlenecks in food supply. We can also determine if predation imposes serious losses to vertebrate and invertebrate prey populations (Stewart et al. 1981; Kitchell and Crowder 1986; Luecke et al. 1990; Stewart and Ibarra 1991; Johannsson et al. 1994; Rand et al. 1995); moreover, we can describe the timing, duration, and location(s) of significant predation, identify the size range of predators that impose the greatest mortality, and define the size range of prey that are most vulnerable to predation. Since these models are physiologically based, they can also be useful for distinguishing between the effects of thermal regime and food supply on growth limitation. Thus, this approach provides managers and researchers with an effective, flexible tool for assessing the relative importance of existing impacts, and enables predictions about how aquatic communities might respond to potential manipulations (e.g., species introductions or enhancement) or environmental change.

The now widely-used Wisconsin bioenergetics model (Hewett and Johnson 1992, and Hanson et al. 1997) provides the core of this approach. The most common application of this model has been to estimate the biomass of food required to satisfy the observed growth of the consumer over specific time intervals. This model has been developed for a number of species, and has become a well recognized tool for managers and researchers. When compared to alternative methodologies, the Wisconsin model has performed well for black basses (Rice and Cochran 1984) and salmonids (Beauchamp et al. 1989, Brodeur et al. 1992, Ruggerone and Rogers 1992, Cartwright et al. 1998) with the model generally producing consumption estimates within $\pm 10\%$ of estimates derived from more conventional, but intensive field-based stomach fullness and gut evacuation methods (e.g., Eggers 1978, Elliott and Persson 1978). Although still very useful, the model has not performed as well for some other species. Where the model has not performed as well, the cause has often resulted from "borrowing" physiological parameters from other species (Ney 1993), or from inadequacies in the data used to describe specific populations or processes.

Improving model performance in future applications and for a broader range of species will require more experimentation and greater attention to the design, implementation, and analysis of field sampling that is dedicated to supplying project-specific inputs to this type of modeling effort. Improving the model's ability to simulate the physiology of specific species will require additional laboratory experiments, particularly those directed at the effects of body size and temperature on maximum consumption rates and on respiration (Bartell

et al. 1986). However, the magnitude of errors generated by these physiological parameters are often insignificant compared to the errors propagated from inadequacies in obtaining and applying field data of consumer growth, diet, thermal experience, abundance (absolute or relative), and survival. Thus, the utility of this modeling approach can be most enhanced by focusing on the key modeling inputs during design and implementation of field sampling efforts.

The purpose of this paper is to present a general approach for quantifying food web interactions and provide brief case studies as examples of the range of questions that can be addressed by this food web modeling approach, and to provide the context for describing the types of data and sampling design considerations that are generally most important for producing defensible simulations of critical trophic interactions within a temporal, spatial, and ontogenetic framework. My colleagues and I have applied this approach to a number of questions in lakes, reservoirs, and streams in western North America, generally involving resident or anadromous salmonids as one of the primary consumers or prey (Table 1). Results from a subset of these studies will be described to demonstrate different capabilities of this approach in the case studies section of this paper, but this will be preceded by a description of the general approach with some emphasis on our current approaches for dealing with issues commonly encountered during the sampling design, implementation, analysis, or modeling phase.

General Approach

Trophic interactions can be quantified by estimating the biomass or number and size distribution of prey consumed by specific consumers in the food web. Consumers are generally categorized by their position in the food web and can be segregated into different life history stages or size categories, based on differences in diet composition. Consumption rates by individuals of each species or life stage of a species can be estimated using a bioenergetics model given estimates of: 1) incremental growth for each age class of consumer; 2) the temporal pattern in diet composition of each age class over the period of interest; 3) the average daily temperatures that the consumer experienced (termed “thermal experience”) over the period of interest; and 4) the energy density of the consumer and prey, and 5) the relative or absolute abundance of predators and prey. The model and suggestions for how data can be acquired and analyzed to provide basin-specific inputs will be described here briefly.

The Bioenergetics Model

The Wisconsin bioenergetics model is an energy-balance model which requires that over any specified time interval, total energy consumption **C** must satisfy the net gain or loss of weight **G** observed over that period plus the metabolic costs **M** and waste losses **W** that accrued over that period. Thus, the most basic form of the model is:

$$\mathbf{C} = \mathbf{G} + \mathbf{M} + \mathbf{W},$$

Or if solving for growth given a known consumption rate (this is rare except perhaps in aquaculture situations):

$$\mathbf{G} = \mathbf{C} - (\mathbf{M} + \mathbf{W})$$

Embedded in each term of this basic equation are formulae which alter energy as functions of body size and temperature. In addition, metabolism **M** includes routine activity costs and specific dynamic action (SDA, the cost of processing a meal), and waste **W** may be scaled directly as a proportion of total consumption. The form and parameterization of these functions vary considerably among species based on laboratory experiments on the physiological processes of consumption, growth, metabolism, and waste. The model provides an estimate of the physiological response of a species, given the size and thermal experience of the organism, whereas the field inputs customize the response of that organism for the situation of interest by specifying the growth, diet, and thermal conditions experienced for each situation of interest. The model operates on a daily time step. Thus, estimates of consumption, metabolic and waste costs, and growth are generated for each day based on

the size and thermal experience of the organism, then the status of the organism (i.e., size and energy density) is updated and computations proceed for the next day in the simulation. Consumption rates can be quantified for daily through annual periods by allowing the simulation to continue through the year or over the entire life span of an organism, if inputs for growth, diet, and thermal experience can be estimated from field data, obtained from reasonable values in the literature, or from on reasonable assumptions based on experience or biological intuition. Clearly, the accuracy and usefulness of these simulations will only be as good as the inputs that are provided. The following sections describe the most important factors that should be considered when designing a sampling program to supply field inputs to the model or when designing a general monitoring program that might support periodic resource assessments using a food web model.

Growth

The model estimates consumption primarily through changes in body weight over specified time intervals of up to a year. Routine monitoring data often provide estimates of annual growth, either by tracking the modal lengths of each age class through time, or by back-calculating size-at-age from otoliths, scales, or other appropriate bony parts. These length estimates can be converted to weight-at-age estimates using length-weight regressions, and thus provide a first approximation of annual weight change by different age classes in the consumer population. These accuracy and precision of these estimates will entirely dependent on ambient variability of the data and the adequacy of the sample sizes. Accuracy and precision of annual growth increments can be improved tremendously by generating size and growth estimates from a relatively short, consistent time of the year.

Aquatic organisms rarely grow at a constant rate throughout the year, because temporal changes in food supply, temperature, and other environmental stressors operate independently or in concert to produce seasonal growth patterns. Since consumption is generally estimated to satisfy the observed growth over specified time intervals, it is important to allocate growth rates as accurately as possible to the appropriate periods of interest during the year. For example, predation on a prey species of concern may be concentrated over a fairly short period (e.g., a week or month) when the predators' growth is either much higher or lower than growth that would be computed from annual average rate. Consequently, errors in estimated consumption on the prey of interest would depend on how much the actual growth of the predators deviated from the average growth rate over the year. Ideally, the mean body weight of each age class could be tracked over each ecologically-significant period of the year, but sample size requirements and logistical or political constraints often preclude the sampling intensity needed to directly measure growth over the period of interest. Thus alternative ways to allocate growth to appropriate periods of the year are often employed. Seasonal changes in condition factor for groups of age classes (e.g., ages grouped as juveniles, subadults, adults, etc.) may allow more temporal resolution in growth allocation with considerably less data than would be required to estimate seasonal growth of each age class directly. For slow-growing, long-lived species (e.g., lake trout), most of the annual "growth" is elaborated as seasonal gain and loss of gonadal rather than somatic growth; therefore, attention to the mean loss in gonadal weight may be the single best estimate of growth for these species. The question then becomes whether adults spawn every year and whether the sex ratio of spawners is highly skewed toward one gender or the other. In general, the important consideration for using population-specific growth to estimate consumption will be whether growth is likely to vary dramatically among seasons for reasons other than simply a physiological response to temperature. If so, then it will be important to allocate weight changes for each age class of the predator into multiple growth cohorts within the year to estimate appropriate consumption rates for each ecologically-significant period.

Diet Composition

Feeding behavior and diet composition of most fishes changes considerably as they grow through various life history stages, occupy different habitats, and respond to seasonal availability of prey. At a minimum, diet composition should be sampled to detect changes seasonally and among size classes of the consumer. Spatial factors may also be influential in determining the diet composition of consumers among habitats (e.g.,

diet differences in nearshore versus offshore zones, Beauchamp 1990, Beauchamp et al. 1992; in the vicinity of tributaries or dams versus other areas during prey migrations Beamesderfer and Rieman 1991, Poe et al. 1991, Rieman et al. 1991; Vigg et al. 1991), but the combined effects of predator movement and prey dispersal may also homogenize the diets from different vertical or horizontal regions of the basin (Cartwright et al. 1998; Baldwin et al. in review).

The temporal scale of interactions can be extremely important when attempting to quantify consumption in response to specific events, and this should be a major consideration when designing a sampling program to measure predation on stocked fish or on a pulse of prey migrating through a population of predators. In systems where we have examined predation on stocked juvenile salmonids, the response has been immediate, severe, and of relatively short duration (two days to two months). Thus sampling should be scheduled to detect whether the magnitude and duration of the predatory response is prolonged or short-lived. We have adopted a strategy of sampling a couple days prior to stocking to measure baseline diet composition of the predators, then on 3 consecutive days after stocking, then once every 2-3 days, followed by a progressively lower frequency of sampling trips. The reduction in sampling frequency can be adjusted by evaluating how quickly the proportional contribution (by weight or volume of the stomach contents) of the prey of interest changes between sampling dates. If the prey disappears from the diet quickly (e.g., within a couple days), then sampling can be reduced to measure monthly or seasonal changes as appropriate. If the diet composition changes measurably, but at a more moderate rate, then a relatively frequent sampling schedule should be maintained (e.g. sample once every 3-7 days) until the prey of interest disappears or stabilizes in the diet.

Diet information for any size class of consumer is entered as an input file into the bioenergetics model as proportional contribution of each prey category in the diet by wet weight (or volume) and the date or range of dates that correspond to each combination of prey in the diet. Consequently, diet data should be recorded as wet weight (or volumetric) proportions of the individual stomach samples. Each nonempty stomach is considered as a separate sampling unit, and the dietary proportions of each prey category from each stomach is averaged with all other nonempty stomach samples corresponding to each size class of predator during each time interval (e.g., season) over the period of interest. This analytical approach gives equal weight to the dietary proportions each nonempty stomach, regardless of the level of stomach fullness. Therefore, a stomach containing a 4-g kokanee (80% of the diet) and 1 g of zooplankton (20%) would be averaged equally with a stomach containing 0.1 g of kokanee bones (20%) and 0.5 g of zooplankton (80%). If these were the only two stomach samples available for that predator-size x time cell, then the average diet composition for that cell would be 50% kokanee and 50% zooplankton. This approach minimizes the influence of the rare stomachs containing large quantities of a particular prey and attempts to reflect the average diet composition of all consumers within the same size x time cell. This method is not without its own set of problems; however, I believe it currently represents the best compromise for reasonable accuracy with reasonable sampling effort. Important assumptions underlying this diet analysis approach can often be evaluated directly through pilot or supplemental studies if deemed important in specific situations. For instance, this approach assumes reasonably similar digestion rates for all major prey taxa, and is sensitive to diel differences in prey composition. Differential digestion is a lesser concern except if temperatures are in the warmer portion of the consumer's thermal range, or if the prey of interest are larval fish, which digest very quickly. Diel differences in prey composition can be important when consumers occupy relatively warm temperatures; however, this concern can be minimized by preliminary sampling to identify when peak stomach fullness occurs (i.e., at dawn, midday, before dusk, after dusk, or at night) and schedule net retrieval or active sampling to maximize the number of samples captured during or after the period of peak stomach fullness.

Thermal Experience

The thermal experience of a consumer can be determined several ways, based on field data or knowledge of their behavior and distribution patterns. For lotic species, average daily temperature recordings from temperature loggers may be sufficient for estimating thermal experience, unless organisms concentrate in thermal microhabitats (e.g., salmonids congregating in groundwater intrusions, etc.). For littoral or warm-water species like black basses, can be assumed to occupy epilimnetic regions of lakes during the summer, and the

warmest (or only) temperatures available during stratification, destratification, and isothermal conditions.

For pelagic, demersal, or species with variable movement and distribution patterns, reconstructing thermal experience is more involved, because the combination of vertical distribution and movement patterns and the concurrent vertical temperature profiles determine the average daily thermal experience of these organisms. If vertical distribution information is available (e.g., diel hydroacoustic depth-specific densities planktivores, or depth-specific catch per effort data from gill nets), then for each sampling date, a weighted mean thermal experience for different species or size classes can be computed by first multiplying the proportion of the catch (for that species or size class) found in each depth interval times the mean temperature in that depth interval, then summing these products over all depth intervals. This sum represents the weighted average thermal exposure for the average individual of that species or size class in the population. When temporal depth distribution data or temperature profiles are unavailable, a commonly-used approach has been to assume “behavioral thermo-regulation” which means that fish will seek out available temperatures nearest their physiological optimum temperature for growth. This may ignore other important behavioral or physiological constraints like foraging opportunities, predator avoidance or tolerance for hypoxic conditions or other suboptimal environmental characteristics.

Energy Density of Predators and Prey

The energy density (in terms of calories or Joules per gram body weight [cal/g or J/g]) of prey will determine how much prey biomass must be consumed for a predator to obtain any given amount of energy. For example, a fish would need to consume at least 1.5 times more biomass of invertebrates with energy densities of 3,000 J/g than fish with 4,500 J/g to acquire the same amount of energy. Moreover, invertebrates generally contain a relatively large fraction of indigestible material in their exoskeleton (averaging 17% of their body weight across many taxa) compared to an average of 3% indigestible material in fishes. Of the energy ingested, waste losses are subtracted and metabolic costs are paid before any energy is allocated for growth. The remaining energy is divided by the energy density of the consumer to convert energy into new consumer biomass. So if a predator's energy density was 6,000J/g, and 4,000 J of energy remained after all waste and metabolic costs were removed, that energy would be converted into $4,000 \text{ J} / (6,000 \text{ J/g}) = 0.67 \text{ g}$ of new growth for the predator.

Energy density varies considerably among organisms, and can change seasonally or with increasing body size. In the Wisconsin bioenergetics model, energy densities are provided as default values in the parameter set for each of the 33 species or life stages provided in the existing model. The consumer's energy is held constant for most species; however, for salmonids and coregonids, energy density increases considerably with increases in body mass up to a threshold weight, then remains relatively constant thereafter. Although strongly recommended, energy densities of predators and prey have rarely been measured in conjunction with a bioenergetic analysis of trophic interactions (but see Luecke and Brandt 1993; Rand et al. 1994; Bryan et al. 1996). Energy densities of prey are generally taken from the literature (e.g., Cummins and Wuycheck 1971; Hanson et al. 1997).

Abundance of Predators and Prey

Ideally, consumption by individuals from each age class is expanded to population-level consumption over daily, monthly, seasonal, or annual time steps, and incorporates the initial abundance and mortality of each age class over the simulation period to provide the best possible estimate of population-level trophic interactions through time. Population-level predation rates can be compared to the temporal abundance of prey populations to determine if predation represents a significant or serious source of mortality. However, abundance of predators or prey commonly represents largest source of uncertainty in most population-level consumption analyses. Although hydroacoustic-midwater trawl assessments of pelagic species like juvenile sockeye salmon, kokanee, coregonids, smelts, and shads have become routine, population estimates for littoral species are often feasible, the efficacy and affordability of population assessments deepwater demersal or pelagic piscivore populations has generally been a major challenge to both managers and researchers. The need to invest in a formal population abundance estimate must often be quite compelling before the expense and political support

can be justified. Despite these uncertainties, several steps can be taken to maximize the value of a food web analysis, evaluate whether a formal abundance estimate is required, and if so, provide strong justification for such an effort.

When consumer abundance estimates are lacking, a useful way to present model simulations is to report consumption demand in terms of consumption per standard unit of the predator population. For instance, if we considered a standard predator population unit of 1,000 predators, ranging in size from individuals in the smallest age class that exhibited predation on the prey of interest through the largest/oldest predators, and allocated these 1,000 predators into size classes in proportion to the size structure observed in the population, then we could multiply individual consumption by each age class by the corresponding number predators allocated to that age class from the pool of 1,000 predators to estimate the total consumption demand of each age class in a standard predator population unit of 1,000. Predation losses could then be reported in terms of the numbers or biomass of prey consumed per 1,000 predators per year or over specific time periods. This approach would also identify which size range of predators actually impose the greatest mortality on prey, because individual size-specific predation rates have been adjusted to reflect the relative abundance of each size class in the predator population. Given this information, managers can decide whether these unit-population predation rates are severe enough to warrant further concern. If so, they will either have sufficient information to proceed with management actions, or the rationale for justifying further examination into the abundance or dynamics of the predator population.

Case Studies

Lake Ozette: Examining Potential Limitations of Competition and Predation on Kokanee and Juvenile Sockeye Salmon

Lake Ozette, located on the Olympic Peninsula in Olympic National Park, Washington, had historically supported a modest run of sockeye salmon that was harvested by the Makah Tribe. The run declined and remained low even after harvest ceased in 1973. Meanwhile, increasing numbers of kokanee began spawning in tributaries previously used by anadromous sockeye salmon, and the remaining sockeye salmon appeared to spawn in the lake. Managers wanted to know if a program to re-establish and enhance anadromous sockeye salmon was feasible. Specifically, had kokanee expanded to fill the niche previously occupied by juvenile sockeye salmon, and would predation losses undermine enhancement efforts. We used the food web modeling approach to examine: 1) how much additional planktivore demand from a sockeye salmon enhancement program could be supported by the zooplankton forage base; and 2) how much mortality could be expected from predation by resident cutthroat trout and northern pikeminnow.

Beauchamp et al. (1995) determined that kokanee and juvenile sockeye salmon represented the predominant source of planktivory in the lake. The combined kokanee-sockeye salmon consumption represented less than 1% of the standing stock biomass of edible-sized (length > 1.0 mm) *Daphnia* in the lake during any month of the April-November growing season. These results did not change dramatically if we assumed that the planktivores could only consume larger (> 1.2 mm) *Daphnia*. Juvenile kokanee and sockeye salmon (40-140 mm fork length [FL]) represented 72% of the diet of limnetic northern pikeminnow ≥ 300 mm FL during winter-summer and 40% of the diet of large (≥ 300 mm FL) limnetic cutthroat trout during spring-summer. Model simulations suggested that for every 1,000 cutthroat trout ≥ 300 mm FL, 139,000 age-0 salmon would be consumed per year. This represented 17% of the average estimated annual fry production. In contrast, only 0.7% of the annual fry production would be consumed annually per 1,000 northern pikeminnow ≥ 300 mm FL. The much lower predation by northern pikeminnow resulted from limited spatial and temporal overlap with juvenile salmonids in the limnetic zone; only 2-8% of the piscivorous northern pikeminnows inhabited the limnetic zone during spring and summer. Beauchamp et al. (1995) concluded that competition was unlikely limit salmonid production, but that predation could potentially undermine enhancement efforts. The predation per 1,000 cutthroat trout was sufficiently severe that it was an obstacle to further enhancement consideration. If managers wished to explore enhancement further, they now knew that some assessment of large cutthroat trout abundance would be needed, and the justification for estimating cutthroat trout density or abundance was the

high per capita predatory demand they represented.

Lake Washington: Estimating Carrying Capacity for Planktivorous Fishes, and Examining Direct and Indirect Effects of Piscivory

Sockeye salmon support a valuable tribal fishery and an extremely popular sport fishery in Lake Washington, but smolt production and adult returns declined in the 1980s and 1990s. In 1980, rainbow trout stocking program was initiated in Lake Washington and was implicated in the decline of juvenile sockeye salmon. Evidence of significant direct predation by rainbow trout on sockeye salmon was minimal and could not explain the decline (Beauchamp 1990). However three piscivores, the native northern pikeminnow and cutthroat trout, and stocked rainbow trout, overlap spatially and temporally to some extent with juvenile sockeye salmon and the other major pelagic planktivorous fishes (longfin smelt and threespine stickleback), so rainbow trout might affect sockeye salmon indirectly by affecting other species in the food web. While the effects of rainbow trout predation were being debated, pilot enhancement efforts for juvenile sockeye salmon were initiated in the 1990s. Managers and scientists were concerned about exceeding the carrying capacity of the lake for the pelagic planktivorous community plus the young planktivorous stages of other fishes in the lake like yellow perch. Thus, the effects of multiple piscivores and multiple planktivores needed to be examined within a food web context to evaluate the relative importance of predation, competition, and temporal food supply on the production of sockeye salmon. Also, limitations to sockeye production needed to be attributed to the appropriate stage of their life history (i.e., mortality during riverine phase for eggs or fry versus lake-phase); thus an analysis of predation on migrant fry was also implemented.

Estimating the Carrying Capacity of Lake Washington for Planktivorous Fishes—Beauchamp (1996) compared temporal changes in biomass, size structure, and production of *Daphnia pulicaria* to consumption demand by the major planktivorous fishes in Lake Washington to determine whether food supply might limit fish production under current or enhanced population levels of sockeye salmon. *Daphnia* biomass and production were estimated from time series of *Daphnia* density, egg ratio, and temperature measurements (Paloheimo 1974; Gabriel et al. 1987) in 0-10 m during 1980-1986, and 10-20 m and 20-58 m during 1984. Consumption demand was estimated from bioenergetic model simulations for different fishes: age-0 sockeye salmon; age-0 and age-1 longfin smelt, rainbow trout, age-0 and age-1 yellow perch, and threespine stickleback. Seasonal data on size-specific diet composition, growth, thermal experience, abundance, and mortality were available from 1983-1991 and data from International Biological Program (IBP) studies during the 1970's. Planktivore predation rates were simulated for April 1989-March 1990, when age-1 smelt were abundant, and for April 1990-March 1991, when age-1 smelt were scarce. Simulations were run with sockeye salmon population abundance set first at current levels, then with projected abundances under different enhancement scenarios. Model simulations estimated that the combined consumption by rainbow trout, yellow perch, and threespine stickleback on *Daphnia* (annual consumption = 978 tonnes) exceeded consumption demand by longfin smelt and juvenile sockeye salmon (882 tonnes in 1989 and 163 tonnes in 1990). During the April-November growing season, combined consumption by all planktivorous fishes represented 0.5-11% of *Daphnia* biomass and 0.2-3.8% of production when sockeye and smelt were abundant, or 0.2-8.0% of biomass and 0.1-2.8% of production when they were scarce. However, *Daphnia* biomass and production were 2-10 times lower in 10-20-m than in 0-10-m depths. If sockeye salmon only had access to this deeper supply of *Daphnia*, their consumption demand represented approximately 30% of *Daphnia* biomass and production in 10-20-m depths when sockeye were abundant in 1989. When they were less abundant in the 1990 growing season, their consumption represented <10% of the *Daphnia* biomass and production in 10-20 m. Simulations of winter consumption indicated that most consumption demand could be attributed to sockeye salmon, followed by threespine sticklebacks and rainbow trout, and that up to 47% of production and 117% of standing stock biomass would be consumed by abundant natural populations if diet compositions remained the same in winter as during the growing season; however, most planktivores likely switched to benthos or more abundant copepods during winter.

Based on these simulations, the importance of the depth-specific availability of zooplankton to sockeye salmon became apparent. Is juvenile sockeye salmon could only utilize *Daphnia* below 10 m during summer stratification, then only modest enhancement of sockeye fry (i.e., no more than a doubling of current production) could be supported by the existing carrying capacity of the lake, and some density-dependent growth reduction might result.

Effects of Piscivory on Planktivorous Fishes in Lake Washington—Longfin smelt is the only other planktivorous fish inhabiting the limnetic zone throughout the year. Smelt live for two years. Although smelt populations were mildly cyclic before 1980, the amplitude of these cycles increased dramatically after rainbow trout stocking began, and even-numbered brood years became 5-15 times more abundant than odd-numbered years (Moulton 1974; Chigbu 1993). Hatchery rainbow trout predation concentrated on longfin smelt, whereas the native piscivores diversified their piscivory among three prey fishes: northern pikeminnow ate considerable amounts of sockeye salmon, longfin smelt, and prickly sculpin, while cutthroat trout ate sockeye salmon, longfin smelt, and threespine sticklebacks.

Patterns of consumption by the three piscivores differed between years when smelt populations were strong or weak. All three piscivore populations began eating pelagic planktivores (25-120 mm prey fork length) when predator fork lengths reached 250-300 mm. Large rainbow trout ate longfin smelt throughout the year (Beauchamp 1990). From model simulations, rainbow trout consumed an estimated 6.3 million (range in prey body mass, 3-18 g) from a strong year class of age-1 smelt, and 4.7 million smelt from a weak year class. Cutthroat trout ate 4.0 million smelt from the strong year class, but only 1.5 million smelt from the weak year class (Figure 3). When the smelt population was depressed, cutthroat trout ate more sockeye salmon parr (2.1 versus 1.4 million; range in body mass 5.0-13.1 g). Northern pikeminnow ate smelt in autumn-winter, and sockeye salmon fry, parr, or presmolts throughout the year. When smelt populations were depressed, northern pikeminnow consumed more sockeye salmon parr (1.7 million) than when smelt were abundant (1.0 million parr eaten), because sockeye parr were substituted for smelt during autumn-winter. The combined predation from the three piscivore populations totalled 10.8 million smelt 2.4 million sockeye salmon parr, and 200,000 sockeye salmon fry during strong smelt years versus 6.3 million smelt, 3.8 million sockeye salmon parr, and 1.2 million sockeye fry during weak smelt years.

Differences between smelt and sockeye in their overlap with sight-feeding piscivores during daylight or crepuscular periods explained the differences in their predation losses and revealed opportunities and constraints for prey-switching by predators. Longfin smelt overlapped extensively with all three piscivores in both time and space, whereas juvenile sockeye salmon overlapped vertically with cutthroat trout throughout the year, seasonally with northern pikeminnow, and only as migrant fry or smolts with rainbow trout. Thus, when longfin smelt were abundant, they absorbed the predation impact by all three piscivores and partially buffered sockeye salmon from predation by cutthroat trout and northern pikeminnow. However, when longfin smelt were scarce, rainbow trout continued to feed heavily on them, driving the population dangerously low, whereas cutthroat trout and northern pikeminnow switched to feed more heavily on juvenile sockeye salmon. Mortality rates for smelt and for the lake-resident phase of juvenile sockeye salmon were nearly doubled in years when age-1 smelt abundance was low compared to when smelt abundance was high. The additional predatory demand imposed by stocked rainbow trout on smelt altered the structure and function of the Lake Washington food web with management implications ranging from lake transparency to the production of commercially- and recreationally-important fishes (Beauchamp 1994).

Riverine Predation on Migrant Sockeye Salmon Fry—Potential riverine sockeye salmon fry predators were sampled once or twice per month in the lower 9.6 km of the Cedar River using a drift-boat mounted electroshocker during the fry migration period in 1983-1985. Of all the species sampled, only wild steelhead smolts contained fry. The proportion of fry in the diet of wild steelhead varied considerably over the migration period, ranging 2-52% and averaging 13% of the wild smolts' diet from February through mid-May. Hatchery-reared steelhead smolts were stocked during the latter half of the fry migration, but no evidence of fry predation was detected from the 18 hatchery smolts that were examined. The heaviest predation occurred during the early to middle portion of the fry migration (February to mid-April), then diets

switched primarily to largescale sucker eggs and invertebrates. Fifty four different bioenergetic simulations were run to examine how uncertainties about predator growth, diet composition, thermal experience, and predator abundance might affect estimates of fry predation. The nominal simulation run which was based on the best estimates of each of the model inputs resulted in an estimated predation rate of 6.8 million fry; the range of estimates from all 54 predation scenarios was 2-44 million fry, but most estimates clustered within 4-10 million fry consumed (Beauchamp 1995). Thus, riverine predation represented a potentially significant source of fry mortality prior to entering the lake, but involved a desirable sensitive native species.

Impact of Non-native Lake Trout in Yellowstone Lake

When lake trout were discovered in Yellowstone Lake in 1994, the National Park Service needed to know whether this non-native predator represented a real threat to the ecological integrity of the Lake and surrounding ecosystem. The immediate questions that needed to be addressed included whether lake trout were naturally reproducing, was the population stable or increasing, and could their trophic interactions alter the dynamics of the native community through competition or predation.

Ruzycki and Beauchamp (1997) used some preliminary diet, distribution, growth, and size structure data collected for lake trout to simulate the seasonal and size-specific loss of the indigenous Yellowstone cutthroat trout due to predation by lake trout. Lake trout ≥ 270 mm FL began including cutthroat trout in their diet. Lake trout were capable of consuming cutthroat trout 50% their own body length, and the average size of fish prey was 25% of the predator's body length. Little was known about the actual abundance of lake trout in Yellowstone Lake, but at least 25 year classes were well represented in the population. Based on the observed size structure of lake trout and the bioenergetic simulations, an estimated 59,000 cutthroat trout (100-300 mm FL) were consumed for every 1,000 lake trout ≥ 270 mm FL. This analysis provided managers important justification and public relations tool for aggressively pursuing a lake trout reduction program, because every lake trout > 270 mm consumed an average 59 cutthroat trout per year. Since the incidental catch of cutthroat trout was high, even when targeting lake trout in time, space, and with larger mesh sizes (Mahoney and Ruzycki 1997), the ratio of lake trout to cutthroat trout catch in these efforts could be viewed in terms of trading off incidental net mortality with reductions in annual predation losses.

Estimating Predation Losses Under Different Lake Trout Population Sizes and Kokanee Stocking Scenarios in Flathead Lake

Flathead Lake historically supported the largest kokanee fishery in North America. This population crashed in the mid-1980s coincident with the establishment of high densities of the opossum shrimp *Mysis relicta* which had invaded from lake upstream where they had previously been introduced (Beattie and Clancey 1991). Also coincident with the mysid increase was a marked increase in lake trout catch and declines in native bull trout and westslope cutthroat trout. Federal, state, and tribal managers attempted to re-establish the kokanee population by stocking up to a million yearling kokanee each spring, but they needed to know whether any of the proposed stocking strategies would result in reasonable adult returns to the fishery and spawning traps. Of primary concern was whether predation losses by lake trout would be too severe to allow sufficient kokanee recruitment satisfy a viable fishery and/or spawning operation.

Bioenergetic model simulations suggested that lake trout predation imposed serious losses on the kokanee population in Flathead Lake, accounting for 87% (in the nominal run) of the number stocked within the first year of their release (Beauchamp 1996). The heaviest predation in 1994 occurred during the first month after stocking 800,000 kokanee (120 mm FL) in June (351,000 kokanee eaten). Kokanee losses during this acute predation period exceeded total predation losses accrued during July-September (263,000 eaten). Lake trout in the 626-750 mm and 501-625 mm size class were responsible for more than 64% of the estimated predation, and 376-500 mm lake trout consumed another 21%. Kokanee disappeared from the diets of progressively larger predators over time suggesting that they rapidly outgrew the smaller, more abundant predators.

Different predation scenarios were modeled to examine the effects of different dietary responses by lake trout, different assumptions about the abundance and size structure of lake trout, and different stocking rates for kokanee. When modeling the effects of either an acute or higher chronic predation response by lake trout, kokanee survival over the first year in the lake declined from 13.2% in the nominal run to 4.6% in a chronic predation scenario, whereas no kokanee survived past midsummer in an acute predation scenario. Lake trout abundance might have been underestimated in model simulations, because size and abundance were based on a hydroacoustic survey in August 1995. Since standard hydroacoustic methods cannot detect fish ≤ 1 m from the bottom, some fraction (e.g., 10-50%) of the predator population might not have been detected. When larger lake trout populations were modeled, kokanee survival (from an initial stock of 800,000) dropped from 13.2% to 4.2% with a 10% increase in lake trout abundance, and no survival was predicted if the lake trout population was 50% larger than the acoustic-based estimate. Model simulations suggested that the kokanee mitigation program could not meet its goals under the current stocking regime of releasing 800,000-1,000,000 yearling kokanee in late spring. Predation losses alone accounted for nearly all of the kokanees stocked, but other sources of mortality would also reduce adult recruitment. Consequently, the kokanee mitigation program was terminated, because predation losses were too high and the expense and limited capacity to raise enough kokanee to swamp the predators was prohibitive.

Discussion

A general approach to modeling aquatic food web interactions was presented with some case histories to demonstrate the types of information that can be gained and the flexibility of this conceptual framework for quantitatively modeling a wide variety of problems. The case histories described above illustrated how food web modeling identified and quantified trophic interactions to determine whether predation, food supply, or competition were important factors limiting survival or production of various species or life stages of interest. These simulations also demonstrated which species or size classes were interacting most strongly, and when the periods of critical interactions occurred. The simulations could then be extended to examine the likely outcome of various scenarios to determine if various management options were feasible and to evaluate whether they might achieve the desired effect. Initial simulations can also be constructed by using existing information from the system, supplemented by literature values and expert assumptions to generate an initial evaluation of the food web. The process of creating a model of the system is extremely valuable, because it allows managers and researchers to formalize abstract concepts of numerous potentially important processes into a visual and mathematical framework. This provides a process for filtering information and a mechanism to identify, quantify, and rank the relative importance of various processes that regulate populations, and thus help managers prioritize efforts to focus on the most critical processes first. This framework helps us to manage uncertainty. It allows us to continue with the analysis by making reasonable assumptions about our uncertainty and placing upper and lower bounds on the range values surrounding our uncertainty. These assumptions are flagged and can then be revisited using sensitivity analyses to quantify how important each particular source of uncertainty might be to the response by the system. For instance, juvenile salmon can represent 0-100% of the diet, but perhaps we can reasonably assume that the percentage in natural conditions will be 10-25%. Rather than allowing paralysis to set in over our lack of information, we can continue by first simulating predation using a some reasonable assumption about the diet composition of the predator, then repeat the simulations with the juvenile salmonid component of the diet that are changed $\pm 10\%$ to evaluate: 1) how much an incremental change in diet translates into a change in predation rate on that prey; and 2) how important is this element of uncertainty. Based on initial simulations constructed from existing information, this modeling framework provides a comprehensive method for identifying and prioritizing management options and establishing the next tier of questions. This provides guidance and the rationale for designing subsequent studies or large-scale experiments within an adaptive management framework, and helps determine when to phase different tasks into the study.

The field effort required to obtain population-specific inputs for the model can be significant, but

some of these activities are often already underway as part of a routine monitoring program. One of the purposes of this paper was to demonstrate the importance of collecting, recording, and analyzing routinely-collected data on relative abundance, length, weight, distribution, diet, age, growth, and basic limnological sampling. Sometimes subtle changes in sampling protocols may vastly improve the utility of the data with only a minor increase in effort.

An alternative and less data-intensive approach is the “qualitative mathematical analysis” described by Dambacher et al. (this volume) which enables an analysis of community stability based on information about whether interactions are positive, neutral, or negative, and has the advantage of incorporating positive and negative feedback loops explicitly into the food web analysis. These quantitative and qualitative modeling approaches each have strengths and weaknesses, but can serve as powerful complementary tools at different phases of a research or management program.

We should continue to strive for better predictive capability in our research and management tools. Some of the key weaknesses in the current modeling framework is that we can only guess at how organisms will respond to changing conditions (e.g., different environmental conditions, changes in the abundance or variety of predator, competitor, or prey species, changes in distribution and behavior of existing species, etc.). To this end, new approaches are being developed to enhance our ability to simulate responses to change, based on mechanistic processes that should drive behavior, but respond predictably to measurable factors. Some examples include visual foraging models for pelagic planktivores (Stockwell and Johnson 1997), and pelagic piscivores (Beauchamp et al. in press). The current planktivore does a nice job of predicting the diel vertical distribution and growth of kokanee in response to the zooplankton density distribution and vertical temperature profiles (Stockwell and Johnson 1997). The pelagic piscivore model predicts how the relative importance of piscivory (or alternatively, the contribution of prey fish to the diet of piscivores) changes as system productivity changes (e.g., water transparency and the density and distribution of forage fishes; Beauchamp et al. in press). Thus, managers could evaluate whether introduction of a new species or other manipulations in stocking, harvest, or enhancement would achieve the desired result or impose new challenges to the ecological integrity of the food web.

Table 1. A list of waters in western states where the food web modeling approach has been applied to various questions about temporal prey supply and demand.

SE Alaska- Margaret Lake: Predation by resident cutthroat trout on stocked sockeye salmon fry (Cartwright et al. 1998).

Lake Washington, Lake Ozette, Washington: Effects of predation, competition, and seasonal food supply on sockeye salmon production (Beauchamp 1990, 1994, 1995, Beauchamp et al. 1992, 1995, in press)

Oregon- Lake Billy Chinook: Effect of native bull trout consumption on kokanee and effect of cannibalism on bull trout recruitment (in preparation).

California/Nevada- Lake Tahoe: Examined the trophic interactions of lake trout and kokanee with regard to the potential for lake trout to regulate populations of native cyprinids, mysids, or kokanee (Thiede 1997), and the ability of kokanee or mysids to regulate zooplankton populations (Van Tassell et al. in preparation).

Montana- Flathead Lake: Model the predatory impact of lake trout on kokanee under current conditions, under various stocking regimes for kokanee, and in response to changes in the abundance or size structure of the lake trout population (Beauchamp 1996).

Wyoming- Yellowstone Lake: Evaluate the impact of non-native lake trout on the Yellowstone Lake ecosystem, particularly on native Yellowstone cutthroat trout (Ruzycki and Beauchamp 1997).

Utah/Idaho- Bear Lake and Strawberry Reservoir: Model the effects of piscivory on recruitment of juvenile Bear Lake-strain cutthroat trout by larger cutthroat trout, rainbow trout, or lake trout, and examine temporal consumption demand versus food supply to identify potential bottlenecks in the production and survival of trout (or kokanee) in oligotrophic Bear Lake versus meso-eutrophic Strawberry Reservoir (Baldwin et al. in review; Orme et al. in preparation).

Colorado River: Evaluate the potential impact of northern pike predation on the endangered Colorado pikeminnow. (Crowl et al. in review)

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